Relationships among carbon dioxide, feed intake, and feed efficiency traits in ad libitum fed beef cattle[1,2]

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ABSTRACT: Angus cattle from 2 beef cattle projects on which carbon dioxide production rate (**CPR**) was measured were used in this study to examine the relationships among BW, DMI, and carbon dioxide traits of beef cattle fed ad libitum on a roughage diet or a grain-based feedlot diet, and to evaluate potential proxies for DMI and feed efficiency. In both projects, the GreenFeed Emission Monitoring system, which provides multiple short-term breath measures of carbon dioxide production, was used as a tool to measure CPR. The data were from 119 Angus heifers over 15 d on a roughage diet and 326 Angus steers over 70 d on a feedlot diet. Mean (±SD) age, BW, and DMI were 372 ± 28 d, 355 ± 37 kg, and 8.1 ± 1.3 kg/d for the heifers, and 554 ± 86 d, 577 ± 69 kg, and 13.3 ± 2.0 kg/d for the steers, respectively. The corresponding mean CPR was 5760 ± 644 g/d for heifers and 8939 ± 1212 g/d for steers. Other traits studied included carbon dioxide yield (**CY**; CPR/DMI) and intensity (**CI**; CPR/BW) and 5 forms of residual carbon dioxide production (**RCP**), which is a measure of actual minus predicted CPR. Feed efficiency traits studied included feed conversion ratio (**FCR**) and residual feed intake (**RFI**). The relationship between CPR and DMI, and between CPR and BW was both positive and linear, for the heifers and also for the steers. For the combined heifer and steer datasets, the R^2 for the relationship between CPR and BW, and between CPR and DMI was 0.82 and 0.78, respectively. The correlation between CPR and DMI (r = 0.84 for heifers; r = 0.83 for steers) was similar to that between CPR and BW (r = 0.84 for heifers; r = 0.87 for steers). Most of the carbon dioxide traits were significantly (P < 0.05) correlated with one or both feed efficiency traits. One of the RCP traits (RCP_{MA}) was computed by maintaining metabolic BW (**M**) and average daily gain (**A**) in the formula for RFI, but substituting the DMI with CPR. The correlation (r = 0.27) between RCP_{MA} and RFI, though significantly different from zero, was not strong enough for its use as proxy for RFI. On the other hand, a strong correlation (r = 0.73) was obtained between the CPR to gain ratio (**CGR**) and FCR. This indicates that, where DMI is not available, CPR could be used in its place to compute a feed efficiency trait similar to FCR, since the computation of CGR was similar to that for FCR, except that DMI was substituted with CPR in the FCR formula.

Key words: ad libitum, carbon dioxide, cattle, efficiency, feed intake

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INTRODUCTION

Energy expenditure of animals is commonly assessed as heat production (**HP**) based on the close relationship between HP and the process of oxidation of organic matter where oxygen is consumed, and carbon dioxide and methane are produced (Kleiber, 1961; Blaxter, 1962; Flatt, 1969). In ruminants, HP is usually assessed by indirect calorimetry which involves measurement of the gases in a respiration chamber, and converting them to heat equivalents (Brouwer, 1965; Whitelaw et al., 1972). Respiration chambers are expensive, labor intensive, and not ideal for testing large numbers of animals. Furthermore, HP computed from respiration chamber data underestimates the energy expenditure of animals in their production setting where they have more space to move around and are exposed to variable environmental conditions. Also animals in respiration chambers are unable to achieve the higher levels of DMI expected from ad libitum feeding in production systems (Bickell et al., 2014; Herd et al., 2016). Hence, there is paucity of information on exhaled gases from free-ranging cattle with ad libitum access to feed in actual production environments.

The GreenFeed Emission Monitors (**GEM**; C-Lock Inc., Rapid City, SD) which provide multiple short-term breath measures have been used to estimate methane and carbon dioxide emissions from cattle under ad libitum feeding in most production settings, such as feedlots, animal houses, and pasture (Arthur et al., 2017; Gunter and Beck, 2018). Bird-Gardiner et al. (2017) provided information on the relationships among methane emission and productivity traits of cattle with ad libitum access to feed, and measured for emissions using GEM units. The objective of this study was to examine the relationships among BW, DMI, and carbon dioxide traits of beef cattle fed ad libitum on a roughage diet or a grain-based feedlot diet, and to evaluate potential proxies for DMI and feed efficiency in situations where individual animal feed intakes cannot be recorded.

MATERIALS AND METHODS

Animals and Management

The data for this study were from projects approved by the New South Wales (**NSW**) Department of Primary Industries and the University of New England Animal Ethics Committees. All animals in the project were managed according to the Australian Code for the Care and Use of Animals for Scientific Purposes (NHMRC, 2013). The data used in this study were derived from 2 separate projects, which used GEM system as a tool to record multiple short-term emissions from cattle on ad libitum feed. One project was on Angus heifers from the NSW Department of Primary Industries, Agricultural Research Center at Trangie, NSW in Australia, referred to as TARC heifers. The second project was on Angus steers from the Angus Beef Information Nucleus (**BIN**), referred to as BIN steers. These 2 datasets were used in earlier publications to provide information on optimizing test procedures for estimating methane and carbon dioxide production of cattle (Arthur et al., 2017), and to report the relationships among methane traits (Bird-Gardiner et al., 2017) derived from multiple short-term emission records from GEM units.

The TARC heifers were raised as calves by their dams on pasture until weaning at approximately 8 mo of age and remained on pasture until tested for methane emissions at an average age of 372 d. The heifers were moved from pasture to the testing unit specifically for the measurement of emissions and feed intake. There were 2 open pens (each approximately 560 m^2) with 2 automatic feed-intake recorders (Bindon, 2001) containing roughage ration and 1 GEM unit in each pen. A total of 121 heifers were available for testing. A maximum of 20 heifers were tested at a time. The heifers were allotted to 7 groups (cohorts) based on similarity of their BW just before the first test. The heifers were provided ad libitum access to a roughage ration which was a commercial blended alfalfa and oaten hay chaff (Manuka "Blue Ribbon" chaff; Manuka Chaff Pty. Ltd., Quirindi, NSW, Australia), containing 88% DM, 17% CP (DM basis), and ME content of 9.3 MJ/kg DM. The pellets used in the GEM units were "Koola Blend," a commercial product (Furneys Stock Feeds, Dubbo, NSW, Australia) with the major ingredients being wheat bran, wheat pollard, and corn (13.3 MJ ME/kg DM and 15.8% CP, DM basis). The measurement period consisted of an initial 21-d period for the heifers to adjust to the roughage ration and be trained to use the automatic feed-intake recorders (for roughage) and the GEM units. This adjustment period was followed by a 15-d test period. The heifers were weighed without fasting at the start of the adjustment period, then weekly until the end of the test. The data recorded during the adjustment period were not included in the analyses.

The BIN steers were measured for growth and feed intake on a feedlot ration at the University of New England “Tullimba” research feedlot, near Armidale, NSW, in Australia.

Nine groups (cohorts) of BIN steers were measured for emissions at the same time as they were being measured for growth rate and feed intake over a standard 10-wk feed efficiency test (Archer et al., 1997; BIF, 2010) at the feedlot, after a standard induction protocol in place at the feedlot. The steers were approximately 554 d of age at the start of the feedlot measurements. Over a 2-wk period, the steers were offered rations of increasing grain content. The steers were then provided ad libitum access to a standard high-grain content–finishing ration that consisted of approximately 80% grain, 10% sorghum hay, 5% protein pellets, plus a proprietary mixture of molasses and water with vitamin and mineral additives (fresh weight basis). The ration had 89% DM, 14% CP (DM basis), and ME content of 11 MJ/kg DM. Each cohort (*n* = 60 to 81 steers) of animals was housed in an open pen (approximately 40 × 50 m) which contained a Growsafe (GrowSafe Systems Ltd., Airdrie, Alberta, Canada) feed-intake recording system and 2 GEM units. For the steers, the pellets used in the GEM units contained sorghum, wheat, and cottonseed meal (12.9 MJ ME/kg DM and 17.8% CP, DM basis) and aniseed flavor as an attractant (Fluidarom 1957; Norel Animal Nutrition, Madrid, Spain). The steers were weighed at the start of the test period and at 2-wk intervals, without fasting. The GEM units and their operation for the BIN project were similar to those for the TARC project, except for differences in the composition of the pellets used in the GEM units, and the fact that the heifers had a more comprehensive training schedule to encourage their use of the units. Information on the operation of the GEM units and training protocols of the heifers and steers are provided in detail in the report by Arthur et al. (2017).

Data and Statistical Analyses

For this study, the data quality recommendation of Arthur et al. (2017) that only cattle with at least 30 CO_2 records, with minimum of 3-min duration per GEM visit per record be used for the computation of carbon dioxide production rate (**CPR**), was implemented for both datasets. The data used in this study were on 119 TARC heifers and 326 BIN steers. Three sets of statistical analyses were done: analyses using heifer-only data; analyses using steer-only data; and analyses using combined heifer and steer data. For the heifers, the ratio of roughage intake to GEM pellet intake was 7.5 to 1. Given the difference in ME of the roughage (9.3 MJ ME/kg DM) relative to the pellets (13.3 MJ ME/kg DM), the total DMI of each heifer was standardized to 10 MJ ME/kg DM, prior to the heifer-only data analyses, as follows:

$$Standardised\ DMI = \left[\left(DMI_{roughage} \text{x } 9.3\ MJ\ ME \right) + \left(DMI_{pellets} \text{x } 13.3\ MJ\ ME \right) \right] / 10 \text{ MJ ME}$$

For the steers, the ratio of the feedlot diet intake to GEM pellet intake was large (54 to 1), and the difference in ME of the feedlot diet (11.0 MJ ME/kg DM) relative to that of the GEM pellets (12.9 MJ ME/kg DM) was small, so no standardization was applied to the DMI for the steers-only analyses. Five different forms of residual carbon dioxide production (**RCP**) were defined to target carbon dioxide production independent of DMI, BW, metabolic BW (**MBW**), a combination of DMI and BW, and a combination of MBW and ADG. The definitions and computational formulae for all the traits used in the study are presented in Table 1. The standard protocol for a feed efficiency test is 10 wk (Archer et al., 1997; BIF, 2010), so the TARC heifers did not have ADG, feed conversion ratio (**FCR**), and residual feed intake (**RFI**) data.

Although the analyses of the heifer-only and the steer-only data were done separately, the same statistical procedures were used for each dataset. To examine the nature (linear or curve) of the relationship between CPR and the animal traits (BW and DMI), an analysis was conducted by fitting linear, linear-quadratic, exponential, and logistic functions to the data from each project as follows:

$$\text{Linear, } Y = b_0 + b_1 x$$

$$\text{Linear} - \text{quadratic, } Y = b_0 + b_1 x + b_2 x^2,$$

$$\text{Exponential, } Y = b_0 + b_1 \mathbf{e}^{-k\,x},$$

$$\text{Logistic, } Y = b_0 + b_1 / \left\{ 1 - e^{-k\,(x-m)} \right\},$$

where Y = CPR, g/d; x is the animal trait (DMI or BW), kg, k is the diminishing constant, b_0 is the constant, b_1 and b_2 are the coefficients of regression, and m is the inflection point. Selection of the preferred function was based on the R^2 values as well as the Bayesian Information Criterion (**BIC**; Schwarz, 1978), which utilizes the significance level of the

Table 1. Definition of traits

Trait name	Abbreviation	Unit	Definition
Body weight	BW	kg	Mid-test weight (Start BW + End BW)/2
Metabolic body weight	MBW	kg	$BW^{0.75}$
Dry matter intake	DMI	kg/d	Daily dry matter intake during emissions test
Average daily gain	ADG	kg/d	(End BW − Start BW)/Days on test
Feed conversion ratio	FCR	–	Ratio of DMI to ADG
Residual feed intake	RFI	kg/d	DMI net of expDMI from BW and ADG, with expDMI obtained by regression of DMI on BW and ADG with cohort as a class effect
Carbon dioxide production rate	CPR	g/d	Carbon dioxide produced per day
Carbon dioxide yield	CY	g/kg	CPR per unit DMI (CPR/DMI)
Carbon dioxide intensity	CI	g/kg	CPR per unit BW (CPR/BW)
Carbon dioxide to gain ratio	CGR	–	Ratio of CPR to ADG
Residual carbon dioxide production from DMI	RCP_D	g/d	CPR net of the expected CPR (expCPR) from the DMI, with expCPR obtained by regression of CPR on DMI with cohort as a class effect
Residual carbon dioxide production from BW	RCP_B	g/d	CPR net of expCPR from BW, with expCPR obtained by regression of CPR on BW with cohort as a class effect
Residual carbon dioxide production from MBW	RCP_M	g/d	CPR net of expCPR from MBW, with expCPR obtained by regression of CPR on MBW with cohort as a class effect
Residual carbon dioxide production from DMI and BW	RCP_{DB}	g/d	CPR net of expCPR from DMI and BW, with expCPR obtained by regression of CPR on DMI and BW with cohort as a class effect
Residual carbon dioxide production from MBW and ADG	RCP_{MA}	g/d	CPR net of expCPR from MBW and ADG, with expCPR obtained by regression of CPR on MBW and ADG with cohort as a class effect

estimated parameters, the variance of the error estimate, and its standard error. The criterion imposes a penalty on more complicated functions for inclusion of additional parameters. The preferred function (e.g., linear model) was then examined further by fitting CPR as the dependent variable and the animal trait (e.g., DMI) as the explanatory variable, with the effects of the other animal trait (e.g., BW), age, and fixed effect of cohort progressively added to the model, to assess their contribution to the model, relative to the simplest model. Pearson correlations among all the traits studied were also calculated after adjustment for the fixed effect of cohort only, as the preferred function analyses had shown that age was not a significant effect when cohort was in the model. The analyses of the combined heifer and steer datasets examined the relationship between CPR and the animal traits BW and DMI (standardized to10 MJ ME/kg DM). All the statistical analyses were conducted using GENSTAT for Windows (Payne et. al., 2015).

RESULTS AND DISCUSSION

Descriptive statistics of the traits studied are presented in Table 2. Information on CPR from cattle in normal production system environments is limited. Although equipment that utilizes multiple short-term breath measures, such as the GEM units used in this study, is relatively new, some studies such as those reported by Herd et al. (2016) and Manafiazar et al. (2017) have used GEM units to measure CPR in beef cattle and by Pereira et al. (2015) in dairy cattle. The heifers from this study had a mean CPR of 5760 g/d and CY of 724 g/kg from 8.1 kg/d DMI of roughage, with a mean BW of 354.5 kg, which is similar to the CPR of 6408 g/d and CY of 794 g/kg from 8.6 kg/d DMI of roughage produced by beef heifers with a mean BW of 344.0 kg from the ad libitum feeding study by Manafiazar et al. (2017). In another ad libitum feeding study (Herd et al., 2016), beef steers and heifers on a grain-based feedlot diet (similar diet used by the steers in the current study) had a mean CPR of 6979 g/d and CY of 582 g/kg from 12.2 kg/d DMI for beef cattle with a mean BW of 454 kg. In comparison, the steers in the current study were heavier (577 kg BW), had higher DMI (13.3 kg/d), and produced proportionally higher CPR (8939 g/d) and CY (679 g/kg). There have been some CPR studies (Boadi et al., 2002; Pinares-Patiño et al., 2007; Stewart et al., 2008) on grazing cattle using the sulphur hexafluoride (SF_6) tracer-gas technique. However, we could not compare our results with those studies as the SF_6 gas technique has been reported to overestimate individual animal CPR, although animal rankings are maintained relative to respiration chamber measurements (Boadi et al., 2002; Pinares-Patiño et al., 2007). The mean for each of the residual carbon dioxide production traits was zero with variation around the mean. This result was expected as per the definition of these residual traits.

The characteristics for the linear and nonlinear models for describing the relationship between CPR and DMI, and CPR and BW for the TARC heifers and the BIN steers are presented in Table 3. For the heifers, there were no differences in R^2 values among the different models for the relationship between CPR and DMI and also between CPR and BW. This is reflected in the BIC values, which indicated that the simpler linear models (with the lowest BIC value) were the preferred models for the heifers. For the steers, the relationship between CPR and BW also showed that the linear model was preferred based on equal R^2 values and the lowest BIC value.

Table 2. Descriptive statistics for the traits studied

Trait[1]	Mean	SD	Min	Max
TARC heifers (*n* = 119)				
Age at start of test, d	371.9	28.3	272.0	424.0
BW, kg	354.5	36.8	246.0	446.0
DMI, kg/d	8.1	1.3	3.6	11.5
Carbon dioxide production rate, g/d	5760	644	4063	7707
Carbon dioxide yield, g/kg	724	106	542	1189
Carbon dioxide intensity, g/kg	16.3	1.4	12.5	19.6
Residual carbon dioxide production from DMI, g/d	0.00	1.01	−2.23	2.68
Residual carbon dioxide production from BW, g/d	0.00	1.01	−2.86	2.82
Residual carbon dioxide production from DMI and BW, g/d	0.00	1.01	−2.17	2.48
BIN steers (n=326)				
Age at start of test, d	553.8	86.4	430.0	764.0
BW, kg	576.5	68.7	428.0	830.0
Metabolic BW, kg	117.5	10.4	94.1	154.6
DMI, kg/d	13.3	2.0	7.4	19.1
ADG, kg/d	1.75	0.30	0.89	2.77
Feed conversion ratio	7.72	1.25	4.94	15.63
Residual feed intake, kg/d	−2.32	1.62	−8.70	1.80
Carbon dioxide production rate, g/d	8939	1212	6045	12833
Carbon dioxide yield, g/kg	679	82	488	1146
Carbon dioxide intensity, g/kg	15.5	1.5	11.9	20.6
Carbon dioxide to gain ratio	5230	803	3537	9179
Residual carbon dioxide production from DMI, g/d	0.00	1.00	−2.66	4.53
Residual carbon dioxide production from BW, g/d	0.00	1.00	−2.69	3.48
Residual carbon dioxide production from MBW[1], g/d	0.00	1.00	−3.62	3.30
Residual carbon dioxide production from DMI and BW, g/d	0.00	1.00	−3.37	3.47
Residual carbon dioxide production from MBW[1] and ADG, g/d	0.00	1.00	−2.73	2.86

[1]MBW denotes metabolic body weight.

Table 3. Evaluation of linear and nonlinear models for describing the relationship between emissions trait and animal traits

			TARC heifers		BIN steers	
Emissions trait	Explanatory variable	Model[1]	R^2	BIC[2]	R^2	BIC[2]
Carbon dioxide production rate, g/d	DMI, kg/d	Linear	0.37	2061	0.47	6322
		Linear-quadratic	0.37	2066	0.48	6321
		Exponential	0.37	2066	0.48	6321
		Logistic	0.37	2071	0.48	6325
Carbon dioxide production rate, g/d	BW, kg	Linear	0.48	2040	0.54	6275
		Linear-quadratic	0.48	2045	0.54	6278
		Exponential	0.48	2045	0.54	6278
		Logistic	0.48	2050	0.54	6284

[1]Model: linear, $Y = b_0 + b_1x$; linear-quadratic, $Y = b_0 + b_1x + b_2x^2$; exponential, $Y = b_0 + b_1 e^{-k\,x}$; logistic, $Y = b_0 + b_1/\{1 - e^{-k\,(x-m)}\}$, where Y = emissions trait, g; x = animal trait, kg, k = diminishing constant, b_0 = constant, b_1, b_2 = regression coefficients, and m = inflection point.

[2]BIC = Bayesian Information Criterion.

For the relationship between CPR and DMI in the steers, the R^2 values and the BIC values were similar among the different models, so the simpler (linear) model is recommended in spite of having a 0.01 lower R^2 value (0.47 vs. 0.48) and a 1 unit higher BIC value (6322 vs. 6321). Most of the studies in the past have been conducted in respiration chambers, and they show that the relationship between CPR and DMI is linear. However, it is known that animals in respiration chambers are unable to achieve higher levels of feed intake expected from ad libitum feeding in production environments (Bickell et al., 2014; Herd et al., 2016). The results of the present study show that with ad libitum feeding of roughage or grain-based diet the relationship between CPR and DMI, and between CPR and BW is also linear.

The results of further evaluation of the linear models for the relationships among CPR, DMI, and BW for the TARC heifers, and among CPR, DMI, BW, MBW, and ADG for the BIN steers are presented in Table 4. Age and cohort had a significant ($P < 0.01$) effect on the relationship between CPR and DMI for both the heifer and the steer datasets. Cohort had a larger effect on the R^2 values than age, for example, the R^2 value obtained for the model which included cohort was 0.70, whereas the one with age was 0.40 (TARC heifer dataset). Additionally, inclusion of age effect when cohort was already in the model did not have any impact on the R^2 value. Hence, models which included cohort effect were preferred as they had the highest R^2 and lowest BIC values. The R^2 value of 0.70 obtained for the relationship between CPR and DMI (with cohort effect) for the TARC heifers on ad libitum roughage diet in this study was slightly lower than the R^2 of 0.79 reported by Manafiazar et al. (2017) for beef heifers on a predominantly silage diet. For the relationship between CPR and BW, cohort was

Table 4. Linear regression models for predicting carbon dioxide production rate from animal traits

Emissions	Order of fitting explanatory variables[2]							Coefficients for significant variables[5]		
trait[1]	First	Second	Third	F – value[3]	F –probability[3]	R^2	BIC[4]	b_0	b_1	b_2
TARC heifers										
CPR, g/d	DMI, kg/d			69.86	<0.001	0.37	2061	3336 ± 294	299.2 ± 35.8	
	DMI, kg/d	Age, d		4.31	0.040	0.40	2061	2211 ± 615	265.9 ± 38.8	3.75 ± 1.81
	DMI, kg/d	Cohort		20.20	<0.001	0.70	2002			
	DMI, kg/d	BW, kg		35.71	<0.001	0.52	2034	1505 ± 401	138.0 ± 41.4	8.85 ± 1.48
	DMI, kg/d	BW, kg	Cohort	22.43	<0.001	0.79	1967			
CPR, g/d	BW, kg			106.02	<0.001	0.48	2040	1485 ± 417	12.06 ± 1.17	
	BW, kg	Age, d		0.98	0.325	0.48	2044			
	BW, kg	Cohort		13.52	<0.001	0.70	2003			
	BW, kg	DMI, kg/d		11.11	<0.001	0.52	2034	1505 ± 401	8.85 ± 1.48	138.0 ± 41.4
	BW, kg	DMI, kg/d	Cohort	22.43	<0.001	0.79	1967			
BIN steers										
CPR, g/d	DMI, kg/d			281.57	<0.001	0.47	6322	3401 ± 334	461.7 ± 24.8	
	DMI, kg/d	Age, d		84.7	<0.001	0.58	6252	2106 ± 329	278.6 ± 26.7	5.65 ± 0.61
	DMI, kg/d	Cohort		28.28	<0.001	0.69	6193			
	DMI, kg/d	BW, kg		111.77	<0.001	0.60	6231	1041 ± 364	210.9 ± 29.0	8.84 ± 0.84
	DMI, kg/d	BW, kg	Cohort	29.98	<0.001	0.77	6093			
CPR, g/d	BW, kg			376.16	<0.001	0.54	6275	1483 ± 387	12.93 ± 0.67	
	BW, kg	Age, d		29.61	<0.001	0.58	6252	1326 ± 372	9.44 ± 0.91	3.92 ± 0.72
	BW, kg	Cohort		32.61	<0.001	0.75	6125			
	BW, kg	DMI, kg/d		53.03	<0.001	0.60	6231	1041 ± 364	8.84 ± 0.84	210.9 ± 29.0
	BW, kg	DMI, kg/d	Cohort	29.98	<0.001	0.77	6093			
CPR, g/d	MBW, kg			373.02	<0.001	0.54	6277	−1099 ± 522	85.42 ± 4.42	
	MBW, kg	Age, d		31.37	<0.001	0.58	6252	−564 ± 508	62.00 ± 5.95	4.00 ± 0.72
	MBW, kg	Cohort		26.22	<0.001	0.75	6231			
	MBW, kg	ADG, kg/d		79.59	<0.001	0.63	6211	−1470 ± 470	68.39 ± 4.40	1357 ± 152
	MBW, kg	ADG, kg/d	Cohort	29.22	<0.001	0.79	6076			

[1]CPR = carbon dioxide production.

[2]MBW denotes metabolic body weight.

[3]For the last explanatory variable fitted in the model.

[4]BIC = Bayesian information criterion.

[5]The intercept (b_0), and the regression coefficients for the first (b_1) and second (b_2) explanatory variables.

significant ($P < 0.01$) for both the TARC heifer and BIN steer datasets. Age was only significant in the BIN steer dataset and its effect did not have any impact on the R^2 value when cohort was already in the model. The preferred models (highest R^2 and lowest BIC values) were those which included cohort.

In this study, the same breed of cattle (Angus) and the same emissions measurement technology (GEM) were used for the 2 projects (TARC heifers and BIN steers). However, the projects were conducted at 2 different locations, with different gender of cattle, and different diets at each location. In general, the nature of the relationships among the carbon dioxide traits and the animal traits (BW and DMI) obtained in this study was similar for the 2 datasets. When the 2 datasets were combined, the R^2 values obtained for the relationship (Figure 1) between CPR and BW, and between CPR and standardized DMI (0.82 for CPR vs. BW; 0.78 for CPR vs. DMI) were slightly higher than those for the individual datasets (Table 4).

Correlation coefficients among all the traits for the TARC heifers and BIN steers are presented in Table 5. Out of the 28 possible pairs of traits, the correlation coefficients of 82% of the pairs were significantly different ($P < 0.05$) from zero for both datasets. Most (4 out of 5 in each dataset) of the nonsignificant ($P > 0.05$) correlations were expected, as those correlations were between RCP traits and their component traits. Most of the significant correlations were positive except 4 in the TARC heifers and 2 in the BIN steers. Carbon dioxide production was strongly ($r > 0.70$) correlated with BW and DMI, and moderately (r from 0.31 to 0.70) correlated with the RCP traits in both datasets. There was a strong negative correlation (−0.79) between CY and DMI in the heifers, which is similar to −0.77 reported by Manafiazar et al. (2017) for beef heifers on a predominantly silage diet. The steers also had a negative correlation between CY and DMI, but it was of moderate strength (−0.66). The residual carbon dioxide production traits were strongly correlated with each other in both datasets, except for the correlation between RCP_B and RCP_D which was moderate.

Feed intake (or DMI) is a trait which is difficult to measure on an individual animal basis for large numbers of animals in their production environment. In the absence of DMI information, the use of proxies have been suggested. In a recent study of beef cattle fed a roughage diet of 1.2 times their maintenance energy requirements and tested for methane and carbon dioxide in respiration chambers, Bird-Gardiner et al. (2018) reported a phenotypic correlation between DMI and CPR of 0.85, with the genetic correlation of 0.95. This highlights the potential for the use of CPR as a proxy for DMI in genetic improvement. The authors of the current study are not aware of any estimates of genetic correlations between DMI and CPR in beef cattle under ad libitum feeding in their production environment. In a study of beef steers and heifers measured for methane and CPR under ad libitum feeding with GEM units, Herd et al. (2016) recommended that CPR can be used as a proxy for DMI to identify animals that emit higher or lower levels of methane relative to their intake in situations where feed intake cannot easily be measured. In the current study, the strong correlation between some of the carbon dioxide traits and DMI in both datasets makes them potential traits to be considered proxies for DMI. It should however be noted that CY, RCP_D, and RCP_{DB} cannot be considered as potential proxies, as their computation required DMI information.

Another common situation where DMI is required is in the evaluation of feed efficiency of animals, where DMI information is combined with

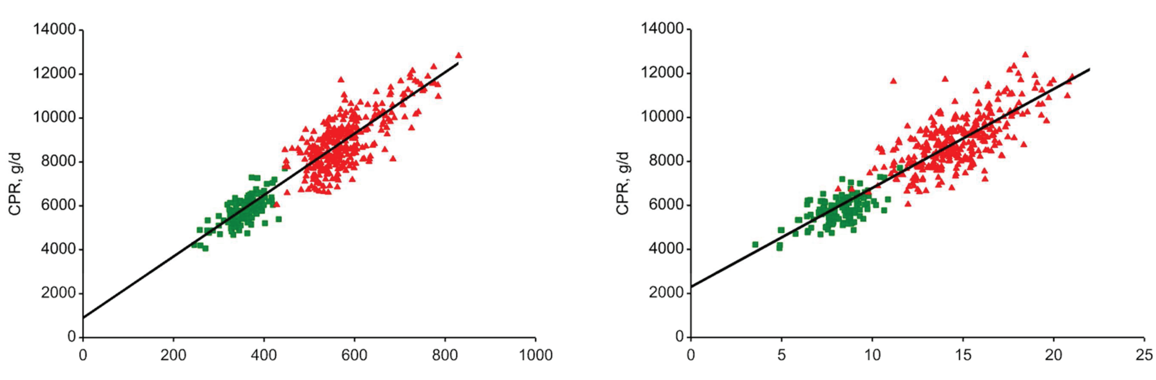

Figure 1. Relationship between carbon dioxide production (CPR) and BW; and between CPR and DMI standardized to ME content of 10 MJ/kg (DMI10) for the combined dataset of TARC heifers (green solid squares) and BIN steers (red solid triangles). The fitted regression line was CPR = 900 + 13.9 x BW (R^2 = 0.82) and CPR = 2297 + 449.8 x DMI10 (R^2 = 0.78).

Table 5. Correlation coefficients[1] among emission and animal traits in TARC heifers (above diagonal) and BIN steers (below diagonal)

Traits	BW	DMI	CPR	CY	CI	RCP_D	RCP_B	RCP_{DB}
Body weight (BW)		0.59	0.84	−0.24	−0.39	0.37	0.00	0.00
Dry matter intake (DMI)	0.54		0.84	−0.79	0.18	0.00	0.36	0.00
Carbon dioxide production rate (CPR)	0.87	0.83		−0.21	0.35	0.55	0.55	0.47
Carbon dioxide yield (CY)	−0.03	−0.66	0.22		0.36	0.38	−0.05	0.32
Carbon dioxide intensity (CI)	−0.12	0.21	0.65	0.41		0.25	0.70	0.58
Residual carbon dioxide production from DMI (RCP_D)	0.26	0.00	0.56	0.62	0.46		0.55	0.85
Residual carbon dioxide production from BW (RCP_B)	0.00	0.21	0.50	0.28	0.70	0.71		0.84
Residual carbon dioxide production from DMI and BW (RCP_{DB})	0.00	0.00	0.48	0.53	0.66	0.85	0.94	

[1]Correlation coefficients with absolute values greater than 0.18 and 0.11 are significantly ($P < 0.05$) different from zero for TARC heifers and BIN steers, respectively.

Table 6. Correlation[1] among carbon dioxide, growth, and feed efficiency traits in BIN steers

Trait	ADG[2]	FCR[2]	RFI[2]
Body weight (BW)	0.43	0.18	−0.01
Dry matter intake (DMI)	0.59	0.30	0.66
Carbon dioxide production rate (CPR)	0.59	−0.01	0.16
Carbon dioxide yield (CY)	−0.09	−0.40	−0.67
Carbon dioxide intensity (CI)	0.30	−0.24	0.24
Carbon dioxide to gain ratio (CGR)	−0.66	0.73	0.02
Residual carbon dioxide production from DMI (RCP_D)	0.28	−0.31	−0.38
Residual carbon dioxide production from BW (RCP_B)	0.42	−0.22	0.28
Residual carbon dioxide production from MBW[3] (RCP_M)	0.42	−0.21	0.28
Residual carbon dioxide production from MBW[3] and ADG (RCP_{MA})	−0.01	0.15	0.27

[1]Correlation coefficients with absolute values greater than 0.11 are significantly ($P < 0.05$) different from zero.

[2]ADG, FCR, and RFI denote average daily gain, feed conversion ratio, and residual feed intake, respectively.

[3]MBW = Metabolic body weight.

BW and ADG to calculate feed efficiency (Arthur et al. 2001; Berry and Crowley, 2013). The challenge has always been the measurement of DMI in the animal's production environment. The BIN steers in the current study were measured for feed efficiency during the same period as they were being measured for CPR. The correlation between the carbon dioxide traits and growth and feed efficiency traits of the BIN steers is presented in Table 6. The correlations between BW and the feed efficiency traits (FCR and RFI) obtained in this study were similar to other published estimates. Arthur et al. (2001) reported low phenotypic correlations between BW and FCR (r = 0.16 for BW vs. FCR) as well as between BW and RFI (r = 0.02 for BW vs. RFI) in Angus cattle. Similarly low correlations were reported by Berry and Crowley (2013; r = 0.01 for BW vs. FCR, and r = −0.03 for BW vs. RFI) in their review of feed efficiency studies in beef cattle. The correlation of 0.30 between DMI and FCR in the current study is similar to the 0.23 obtained by Arthur et al (2001) and the 0.39 obtained by Berry and Crowley (2013). Arthur et al. (2001) and Berry and Crowley (2013) reported a correlation of 0.72 between DMI and RFI, which is similar to the 0.66 estimate obtained in this study. Most of the carbon dioxide traits were significantly ($P < 0.05$) correlated with one or both feed efficiency traits (FCR and RFI), except the nonsignificant correlations between BW and RFI, CPR and FCR, and CPR to gain ratio (**CGR**) and RFI. The strongest correlation obtained (r = 0.73) was between CGR and FCR. The computation of CGR was similar to that for FCR, except that DMI was substituted by CPR in the FCR formula. This indicates that, where DMI is not available, CPR could be used in its place to compute a feed efficiency trait similar to FCR. A similar approach was used in the computation of RCP_{MA}. The DMI in the formula for RFI was substituted with CPR to generate RCP_{MA}. The correlation between RCP_{MA} and RFI (0.27), though significantly different form zero, was not strong enough for its use as proxy for RFI.

With the availability of equipment such as the GEM, for measurement of exhaled and inhaled gases by livestock in their production settings, it is worth revisiting earlier approaches that assess energy expenditure (Brouwer, 1965; Whitelaw et al., 1972) of the animal to estimate energy intake. In addition to measurement of oxygen, carbon dioxide, and methane by equipment such as the GEM, other measurements on animals will be required to estimate retained energy, e.g., fat deposition, ADG.

The results of this study show that under ad libitum feeding of roughage or grain-based diets the relationships between CPR and DMI, and between CPR and BW are both strong, positive and linear. This indicates that as the quantity of feed consumed increases, the amount of carbon dioxide produced also increases. The same strong, positive and linear relationship was observed when the roughage and grain-based diet data were combined and standardized to 10 MJ MEI. These results indicate that under ad libitum feeding situations where DMI cannot be measured, CPR can be used to identify cattle with higher or lower DMI and those with higher or lower feed to gain ratio with a reasonable level of effectiveness. Further research is required to improve the accuracy of estimation of DMI and should include strategies which take into account information on CPR as well as the other gases (e.g., methane and oxygen) measured by equipment such as the GEM, as well as information on retained energy (e.g., fat deposition, ADG) by the animal.

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